Technical Report No. 54

INTEGRATED ISLAND ECOSYSTEM ECOLOGY IN HAWAII

INTRODUCTORY SURVEY

Part I of Proposed Synthesis Volume
for US/IBP Series

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Preface

This is the draft manuscript of Part I of our synthesis volume. It is reproduced only for distribution within our group so that each Hawaii IBP participant will have an idea of what we are putting down before our volume appears in print. We intend to do the same with the other parts as they come out.

For Chapter 3 I drew heavily on our original IBP proposal. This chapter reflects the efforts of several individuals, including A.J. Berger, Sheila Conant, Allison Kay, C.H. Lamoureux, J.L. Gressitt, F.R. Fosberg, F.J. Radovsky, and others. But also the ideas put down in the other introductory chapters reflect the thinking that developed through our activity as a research team.

Authorship for sections in the synthesis volume, therefore, must be viewed more as responsibilities assigned to us as writers and editors rather than (in the traditional sense) as authorship of a piece of original research. This applies to all remaining synthesis parts, chapters, and sections.

The manuscript may still be subjected to several editorial changes before final printing. I would appreciate comments on the manuscript. Please transmit them to me.

D. Mueller-Dombois
January 1975

ABSTRACT

This report is a draft manuscript of Part I (Introductory Survey) of the synthesis volume of the US/IBP Island Ecosystems Stability and Evolution Subprogram. Further parts to follow are:

Part II	Spatial Distribution of Island Biota
Part III	Temporal Relationships of Island Biota
Part IV	Community Structure and Niche Differentiation
Part V	Genetic variation within Island Species
Part VI	General Conclusions

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PART I. INTRODUCTORY SURVEY

This book is a synthesis of the methods and results of 36 investigators who used a team approach to study selected island ecosystems in Hawaii. The research was initiated in September 1970 under the auspices of the International Biological Program (IBP) as one of the U.S. Environmental Component Studies. In that component the Hawaii IBP represented one of three subprograms of the Origin and Structure of Ecosystems Program and was known as the ISLAND ECOSYSTEMS STABILITY AND EVOLUTION Subprogram. The subprogram was financed almost entirely by the National Science Foundation.

At the time of writing, the Hawaii Island Ecosystems Subprogram had been in progress for a period of four years. Progress was reported in a series of technical reports.

The Technical Report Series begun in December 1970 had yielded more than 50 individual reports. These are now permanently available on microfiche. Throughout this synthesis volume reference is made to individual technical reports. These are cited as TR (Technical Report) numbers (e.g. TR 16) in place of author names and dates. A list of the running numbers and topics of technical reports is appended to this volume. To obtain a report on microfiche, please write to:

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CHAPTER 1

SCOPE AND OBJECTIVES

The broader research aims of the Hawaii IBP were twofold: (1) to concentrate on aspects that are unique and different in island ecosystems as compared to continental ecosystems and (2) to assist in solving regional problems relating primarily to wildland management and conservation of biological resources.

On this basis, <u>four general objectives</u> were defined as follows:

1. To determine why some organisms in Hawaii have undergone speciation, while some of the most successful have not.
2. To determine why some ecosystems in Hawaii are stable, some fragile.
3. To develop models relating to the variables that contribute to stability and diversity in Hawaiian ecosystems.
4. To determine the rates of evolution in different organism groups in Hawaii and the factors affecting these rates.

These four objectives required research approaches in two different disciplines: (1) studies in evolutionary biology, microevolution, and ecological genetics (objectives 1 and 4) and (2) studies in ecosystem and general ecology (objectives 2 and 3). One of our challenges was to integrate these two basically different areas in a combined study approach.

For each objective we established <u>initial working hypotheses</u>:

<u>To objective 1</u>

(a) That speciation is the result of biological hardship.

(b) That speciation occurs only if the population develops isolating mechanisms.

(c) That speciation occurs only if the population develops in areas of geographic isolation.

(d) That successful nonspeciated populations have larger gene pools.

To objective 2

(a) That species diversity is positively related to stability.

(b) That life-form diversity may be more important to ecosystem stability than species diversity.

(c) That climatic factors have significant effects on stability.

(d) That native ecosystem stability is directly related to the vigor (= height and density) of the two major native tree species, *Metrosideros collina* subsp. *polymorpha* and *Acacia koa*.

To objective 3

(a) That Hawaiian ecosystems may be modelled for predicting the outcome of alterations.

(b) That Hawaiian ecosystems may be modelled for comparison of their structures with those of continental ecosystems and other island ecosystems.

To objective 4

(a) That speciation is a function of time.

It was obvious from the start that these objectives and hypotheses could not receive a complete treatment within the four-year time frame given for our project. Instead, they must be viewed as longer-term objectives. We restricted our research to a few case examples and to a subset of the four longer-term objectives. This subset is expressed in our four synthesis themes:

PART II Spatial distribution of island biota

PART III Temporal relationships of island biota

PART IV Community structure and niche differentiation

PART V Genetic variation within island species

CHAPTER 2

GENERAL CHARACTERISTICS OF ISLAND ECOSYSTEMS

Island biota have received considerable attention from evolutionary biologists since Darwin (1859) developed the theory of speciation from his observations of the Galápagos finches. Carlquist (1965, 1970, 1974) presented comprehensive reviews together with theories that may explain the often bizarre life forms developed on isolated islands. MacArthur and Wilson (1967) considered island ecosystems ideal laboratories for the development of evolutionary theory. Fosberg (1963, 1966, 1967), Dorst (1972), and others (e.g. UNESCO Expert Panel on MAB Project 7, 1973) have written conceptual papers dealing with the precarious balance and fragility of island ecosystems.

There are three important ecological conditions that render island ecosystems different in degree from continental ecosystems. These are (1) geographic isolation, (2) small size, and (3) recent time.

2.1 Geographic Isolation

This condition is responsible for a "screening effect" on the number and kinds of organisms that can reach an island. A small percentage of these becomes established as populations which may then "radiate" into the various habitats available on an island. In time, a successfully radiating population may become adapted by specializing. The original population may thus become differentiated or fragmented into a number of subpopulations. The result is the often made observation on high islands that related taxa have an unusually wide ecological amplitude. The screening effect itself, however, results in biotic disharmony in the sense of "missing taxa." This means that certain taxa and life forms that one may expect to find in environmentally equivalent habitats on other islands or on neighboring continents are absent altogether.

This leads to the question of community saturation and the resultant stability-fragility relationships. The two phenomena work against each other: disharmony suggests nonsaturated conditions, radiation suggests a filling effect with respect to available habitats and niches. The stability-fragility relationships in island ecosystems are not so easily predicted (as are often attempted on a more casual basis) because community saturation depends not only on taxonomic diversity, but on the ecological characteristics of the participating taxa as well. Study of the ecological roles of such taxa requires detailed and intensive research.

2.2 Small Size

As a rule, islands are thought of as small land masses surrounded by water. Different opinions exist with regard to defining Australia as an island or a continent; but, for the purpose of studying differences between island ecology and continental ecology, islands should be defined as small land masses surrounded by water. For island research the UNESCO Expert Panel on MAB 7 (1973) suggested an approximate upper size limit of 10,000 km^2--a limit which includes the Island of Hawaii (the largest island in the Hawaiian archipelago).

The biological implication of "small land size" is that population sizes of perennial organisms also tend to be small. Even in the mountainous or high islands, which usually have much greater land masses than low coral islands or atolls, the recurrence of similar habitats is rather limited in comparison to most continental mountain ecosystems. Small areas restrict the size as well as the gene flow and composition of populations developing there. Greater genetic homogeneity may imply increased specialization. Whether or not this leads to a greater fragility of island populations cannot be answered as generally as is usually done, because population stability depends on both the ecological properties of the population and the nature of the regional perturbations.

2.3 Recent Age

One biological consequence of recent geological age is that tropical island rain forests on high volcanic islands are much younger than most tropical continental forests. In certain areas the latter may have undergone more or less uninterrupted succession from giant equisetum-lycopod and seed fern forests to primitive gymnosperm and angiosperm forests. In contrast, the origin of most existing forests on high volcanic islands is within the modern angiosperm era. For example, the oldest parts of the high Hawaiian Islands are estimated to be merely six million years old (Macdonald and Abbott 1970). Fosberg (1948) estimated that only one arrival form was required to become successfully established every 20,000 to 30,000 years to account for today's native angiosperm flora of a little over 1,700 taxa. The shorter geological time available for community development may in part account for a lower diversity in tropical island as compared to tropical mainland communities. In that respect tropical island communities are similar to temperate mainland communities, which can be considered species-depauperate compared to tropical continental communities (Doty et al. 1969).

2.4 Unique Evolution

It may be argued that the three ecological conditions mentioned above are not unique to islands. However, the biological consequences of these three conditions are most clearly developed on islands. The main point is that these conditions have resulted in a different evolution in island ecosystems. Thus, on islands, more so perhaps than in biogeographically different continental ecosystems, the effect of a unique evolution becomes evident in many ecological relationships. The ecological relationships involve primarily the interactions among native species, and among native and exotic species. Many of the exotic species were introduced by man within the last 200 years. Man thus effectively broke the natural isolation barrier of the Hawaiian Islands.

2.5 Community Structure

Because of unique evolutions and species assemblages on islands, the structure of island communities is expected to be unique also. However, this is true only at the level of species composition and quantitative distribution. At the level of dominant plant life form, islands are not at all unusual. Nearly all world plant formation types can be found on high islands. There are grasslands, bogs, alpine tundras, savannas, closed evergreen rain forests, open seasonal forests, scrub formations, and deserts, to name a few of the more common world formations or biome types. These are conditioned by the peculiarities of climates and soils just as they are on continents. This gross-structural similarity combined with the unique evolution of island biota and communities establishes the scientific and practical relevance of deriving general principles from the study of island ecosystems.

CHAPTER 3

SOME BIOLOGICAL AND ENVIRONMENTAL CHARACTERISTICS OF THE HAWAIIAN ISLANDS

3.1 Biogeography

The native Hawaiian biota is the product of several million years of evolution on an isolated chain (Fig. 3.1) of volcanic islands extending 2400 km (1500 miles) northwest to southeast, from 28°N to 18°N latitude, in the Pacific (Fig. 3.2). Surrounded by deep water (>5000 m deep), the islands' nearest neighbors are Johnston Island--720 km (450 miles) southwest, the Line Islands--1600 km (1000 miles) south, and Wake Island--1930 km (1200 miles) to the east. This extreme isolation of the island chain has undoubtedly been the most influential of all the factors which have contributed to the development of a terrestrial flora and fauna unique as to disharmony and speciation.

The native terrestrial biota, now estimated at between 10,000 and 15,000 species, probably descended from less than 1000 introductions which must have colonized the islands against very great obstacles. Many groups of plants and, especially, animals dominant or abundant on other Pacific islands and on the continents bordering the Pacific are absent from the Hawaiian chain. Other groups occur as strays or relicts. Still others which are rare elsewhere are dominant in Hawaii. Representation apparently reflects, in part, superior vagility (propensity for dispersal) over long distances by wind, water, or long-ranging sea birds. This thesis is supported by the noticeable lack of native nonflying mammals, land reptiles, amphibians, and freshwater animals in general, by the presence of plants, many of which must have originally had small seeds adapted to wind and bird dispersal (Carlquist 1966a, 1966b), and by the capture of certain insects and spiders in air traps over the ocean (Gressitt and Yoshimoto 1964).

Speciation rates during the course of evolution of the native biota have differed among the various endemic groups of flora and fauna. In the case of the single bat (Lasiurus cinereus semotus) found in the islands, there has been no local speciation. Among the birds, where 70 kinds have apparently evolved from 15 ancestors, speciation has been moderate but nevertheless remarkable. In other instances large numbers of species have presumably evolved from single ancestors. The insect family Drosophilidae, with 600-700 species (Carson et al. 1970, Hardy 1974), and the plant genera Dubautia, Argyroxiphium, and Wilkesia are examples of this.

Many factors have influenced speciation. These include such isolating mechanisms as different times of arrival, variations in gene pools (through perhaps a single gravid female, egg batch, or seed), differing success in the new environment, and different situations with respect to genetic trends, population levels, adaptation, competition, and parasitism. Speciation has also been influenced by age differences between the islands. The distinctive chronological gradation so noticeable in the topography (from northwest to southeast within the archipelago) is reflected in the biota of the islands. Many other features of the archipelago serve as isolating mechanisms. These include small offshore islands, kipukas (older vegetation surrounded by recent lava flows), lava tubes, and narrow valleys on the older high islands (Kauai, Oahu, Molokai, and Maui).

Since the advent of man in Hawaii, profound ecological changes have taken place. Large numbers of "weed" or "pest" species have been introduced, both intentionally and accidentally. Many plants which are common garden ornamentals or hedges elsewhere have become serious weeds, blanketing large areas cleared of forest for grazing, and invading native forests.

Similarly, various mammals and birds have been introduced as escaped pets. Others have been released by organizations or local government agencies

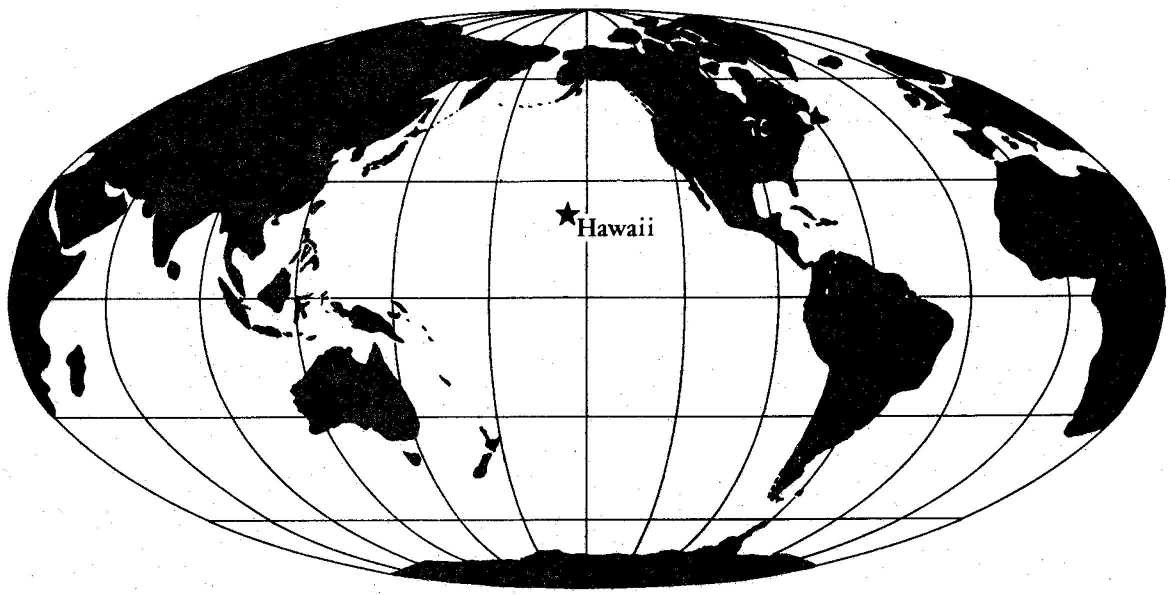


FIG. 3.1. Map showing the location of Hawaii in a global perspective.

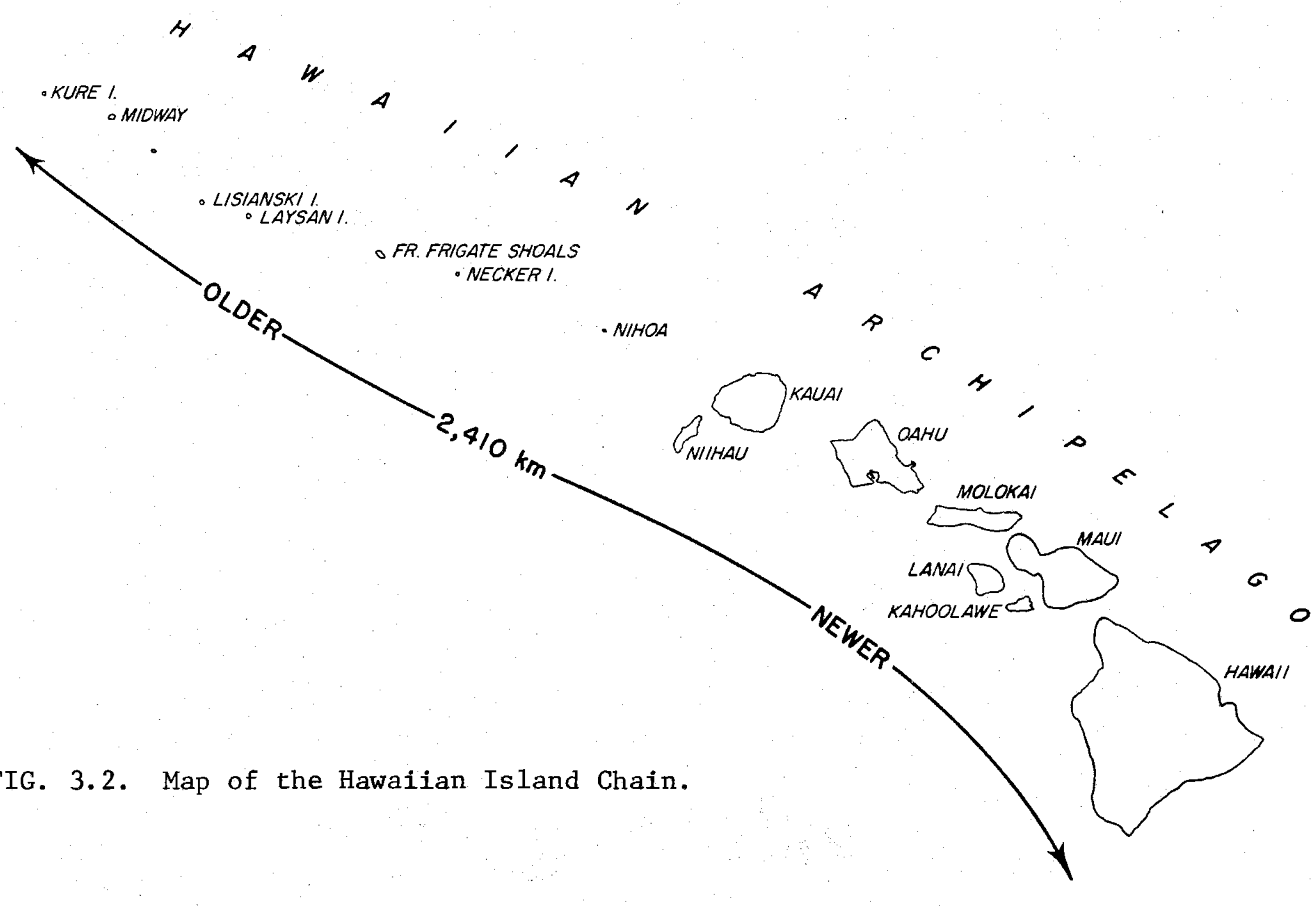


FIG. 3.2. Map of the Hawaiian Island Chain.

for hunting purposes. Cattle, horses, goats, sheep, deer, and pigs have devastated thousands of acres of natural vegetation and continue to threaten some of the remaining stands. Mongooses and rats have helped reduce native birds. Many species of insects and other invertebrates have also ravaged the native environment. An average of 16 insect species is accidentally introduced to the islands each year (Beardsley 1962).

The transformation of the biota from native to introduced is not restricted to the lowlands, but extends to mountain ridges, valleys, and summits, where hiking trails, sightseeing roads, radar, and other man-associated phenomena occur. Many temperate plants such as Rubus have become established in these areas. Native plants have disappeared and been replaced by the invaders in practically all areas where the original vegetation was cleared to make way for towns, roads, agriculture, grazing, gardening, and other developments. Exceptions occur where special precautions such as fences (effective for only a few of the invaders), weed-control, or other special measures have been taken.

Associated with the recession of the native vegetation from the lowlands and parts of the mountains is the decrease in the numbers of native birds, insects, and snails, and the extinction of some of these species. It has become obvious that native animals cannot survive when the vegetation of their natural habitat is seriously disturbed.

3.2 Volcanism

The Hawaii Chain is estimated as twenty-five million years old in the northwest (Midway Island) and is progressively younger toward the southeast (see Fig. 3.2). Ages of the older sections of the high islands (estimated by the potassium-argon method) are as follows: Kauai 5.6, Oahu 3.3, Molokai 1.8, Maui 1.3, and Hawaii 0.8 million years old (Macdonald and Abbott 1970). At the southeast end, on the Island of Hawaii, lava still bubbles or fountains forth and runs down toward the sea. Thus, at one end of the island chain one finds mountains with freshly cooled basalt lavas covering much of the land surface; and at the other end one finds only sandy, largely nonigneous, calcareous atolls or very low islands. All stages are to be found in between. Kauai, the oldest major high island, has old soil types and relatively species-rich communities; Hawaii, the youngest major island, appears to have the simplest biotic communities, with some surfaces as yet unpopulated.

As lava flows from the tops of mountains, it leaves a chemically uniform belt-transect of new volcanic surface stretched downward through a great range in climate. Alongside such lava flows one often finds mature communities which may serve as standards toward which the sere on the new lava flow can be expected to progress. This enables one to study community development on the same substratum through a wide variety of climatic conditions. Such uniform surfaces range in age from prehistoric to historic (historic refers to the last 200 years). Thus one can study the results of seral development in a given climate on substrates at different ages over the past few hundred years.

Another interesting phenomenon associated with lava flows is the formation of kipukas--islands of vegetation. Molten lava flows like water toward the lowest elevation. Consequently, when lava flows around hills, islands of older lava remain which may be heavily forested. Successive eruptions from different vents in a rift zone may result in kipukas bound by lava flows of different ages and at different stages of revegetation. Kipukas may also occur at the leading edge of a particular lava flow which stopped because the eruption came to an end. Other types of kipukas may be formed by the general vagaries of lava flows. In addition to providing sites of different stages of succession under similar climatic conditions, kipukas are prime areas for finding endemic plants and animals.

The Hawaiian lavas are highly vesicular basalts which differ in gas and heat content. The hotter, more gaseous lava type is called pahoehoe. Pahoehoe flows like a river during an eruption. It chills with a smooth or ropy surface. The cooler, less gaseous lava type is calles a'a. A'a moves more sluggishly than pahoehoe and has a highly fractured clinkerlike or rock-rubble surface.

When it flows, pahoehoe lava usually roofs over with a cooling crust. The roofing process insulates the flowing lava from atmospheric cooling and thus enables the lava to flow great distances from the vent. These roofed-over crusts often form channels that partially drain, creating a system of lava tubes or caverns within the flows. Older lava tubes develop into discrete ecosystems with many species of highly specialized obligatory cavernicoles related to endemic surface species. These lava tube ecosystems offer a rich area for evolutionary and ecosystem research, including comparisons with continental cave ecosystems.

3.3 Climate

Hawaii is the only state in the U.S. which lies within the tropics. It is also the only state composed of relatively small islands completely surrounded by ocean. These facts contribute to its unique climate.

Descriptions of the macroclimates of Hawaii have been provided by Blumenstock (1961), Britten (1962), Price (1966), and Bumenstock and Price (1967). They describe the main Hawaiian Islands as the summits of volcanic mountains that arose from the bottom of the sea (Fig. 3. 3). The mountainous nature of Hawaii is indicated by the fact that 50 percent of the state land area lies above an elevation of 600 meters (2000 feet), and 10 percent lies above 2100 meters (7000 feet). The maximum elevations (in meters) of the six major islands are: Hawaii - 4206; Maui - 3055; Kauai - 1597; Molokai - 1515;

Oahu - 1231; Lanai - 1207.

Almost half the land in the state lies within 8 km (5 miles) of the coast. Only about 5 percent, all on the island of Hawaii, is more than 33 km inland. Thus the marine influence on the climate is pronounced.

During most of the year the northeast trade winds account for the dominant air movements over the state, and rainfall distribution is influenced primarily by the trades and the terrain. From May through September the trades are prevalent 80 to 95 percent of the time. From October through April the trades are prevalent only 50 to 80 percent of the time. Major storms, associated with cold fronts, lows, and upper air lows and troughs occur, on the average, from two to seven times per year, usually between October and March. It is during such winter storms that dry leeward lowlands receive most of their annual rainfall. In fact, most areas of the state, except for the Kona coast of Hawaii, have higher rainfalls in the winter than in the summer, although most areas with high rainfall remain relatively wet all year. Hurricanes may occasionally pass close to Hawaii, but between 1904 and 1967 only four came close enough to affect the islands, and only one actually passed through the islands. Tornadoes also occur at infrequent intervals.

Day length in Hawaii is relatively uniform throughout the year. In Honolulu the longest day (including twilight) is 14 hours, 10 minutes; the shortest is 11 hours, 40 minutes. The uniform day length and the small annual variation in the altitude of the sun above the horizon result in relatively small variations in the amount of incoming solar energy. This and the nearly constant flow of fresh ocean air of relatively uniform temperature over the islands are the major factors which contribute to the very slight seasonal changes in air temperature in the islands.

The overall pattern in Hawaii is one of equable temperature conditions. Below 1523 meters (5000 feet) the difference in mean monthly temperatures between warmest and coolest months does not exceed 5°C, while the average daily range in temperature is between 4° and 9°C. The highest temperature on record is 38°C (100°F), but temperatures above 35°C (95°F) are extraordinarily rare even in the dry leeward lowlands, and outside such areas temperatures of 32°C (90°F) and above are quite uncommon. The lowest temperature on record is -10°C (14°F), recorded at 3055 meters (10,020 feet) on Haleakala, Maui. When long-term records from the summits of Mauna Kea and Mauna Loa, above 4115 meters, are available, it is possible that temperatures as low as -15°C (5°F) or less may be recorded.

Under trade wind conditions a temperature inversion is typically present between about 1523 and 2130 meters (Fig. 3.4). This inversion layer is correlated with a moisture discontinuity and has an effect on both relative humidity (RH) and rainfall. Below the inversion the RH commonly averages 70 to 80 percent in windward areas and 60 to 70 percent in leeward areas. Above the inversion the relative humidity is generally below 40 percent and often as low as 5 to 10 percent.

While the average annual rainfall of the state as a whole is about 1880 mm (70 inches), variation from place to place is so great as to make this figure meaningless. At Kawaihae on the leeward coast of Hawaii the average annual rainfall is less than 170 mm; at Mt. Waialeale on Kauai it is 12,350 mm (and has exceeded 15.2 m!). Rainfall gradients are extremely steep, exceeding 100 mm per km in many places. Along the 4 km line from Hanalei Tunnel to Mt. Waialeale on Kauai the gradient is 1800 mm per km. In general, leeward lowlands and mountain peaks above 2500 meters elevation are the driest areas, while maximum rainfalls are recorded at or near the crests of mountains less than 1800 meters high, and at 610 to 1220 meters on the windward slopes of the higher mountains.

TABLE 3.1 Soil orders in the Hawaiian Islands

Soil Order	Description	Occurrence
A. Well-developed soils in humid climates (i.e. lateritic soils)		
(1) Oxisols	Strongly weathered oxide soils; formerly Low Humic Latosols	Relatively flat land at low elevations
(2) Ultisols	Ultimately leached soils; formerly Humic Latosols, Hudrol Humic Latosols, and Humic Ferruginous Latosols	Steeper slopes and less stable landscapes at somewhat higher elevations than oxisols; montane tropical rain forests on older higher islands
(3) Spodosols	Spodos = woodash = Podzols	Bog and swamp soils in high rainfall zones, e.g. Alakai Bog soil on Kauai
(4) Alfisols	Much like Ultisols but less leached of nutrients; Al-Fe soils or formerly Ped Alfer soils	NW Oahu in subhumid climate under forest
B. Well-developed soils in seasonal or dry climates (partly calcified)		
(1) Aridosols	Formerly Red Desert soils	Very dry zones, mostly confined to the northern leeward shore of Hawaii Island; annual rainfall less than 200 mm
(2) Vertisols	Vert = inverted; soils that swell and shrink with wetting and drying; formerly Dark Magnesium Clays or Grumusols	Several places in lowlands on leeward Oahu, especially on talus slopes and floors of deeply dissected amphitheater-headed valleys
(3) Mollisols	Moll = soft; soils with deep, crumb-structured A_1 horizons; rather rich in nutrients; in part formerly Latosolic Brown Forest soils	Moderately dry climates (e.g. soils of Kipuka Ki and Kipuka Puaulu on IBP transect 1 in Hawaii Volcanoes National Park)
C. Little-developed or geomorphically recent soils		
(1) Histosols	"Organic tissue" soils; shallow soils of predominantly organic materials (5-20 cm deep); recent counterpart to Ultisols	Overlying relatively recent lava; under rain forests; mostly on the Island of Hawaii
(2) Inceptisols	Incipient = young soils, but not very recent; from volcanic ash with weakly developed horizons	Cover extensive areas on Hawaii on the slopes of Mauna Kea and in Hawaii Volcanoes National Park; also on East Maui
(3) Entisols	Ent = recent; lacking horizons; formerly Regosols	On volcanic ash near tree line on Mauna Kea and Mauna Loa; on old beach sand (N. Oahu); on recent alluvial deposits
(4) Lithosols	Lithos = rock; essentially rockoutcrop, includes all recent lava flows (a'a and pahoehoe) and older rock bluffs and stony substrates. This name not used officially among new Hawaiian soil orders, but seems to fit the category "Miscellaneous land types"	Dominant surface on Mauna Loa and Kilauea volcanoes; older rockoutcrops occur locally in the mountains of all high islands

TABLE 3.2 List of the best-represented families and genera in the native angiosperm flora of the Hawaiian Islands

Family	Approximate Number of Species and Varieties	Genera with Largest Numbers of Taxa
Compositae	200+	Bidens, Dubautia, Lipochaeta
Gesneriaceae	200+	Cyrtandra
Campanulaceae subfamily Lobelioideae	150+	Cyanea, Clermontia, Lobelia
Rubiaceae	100+	Hedyotis, Gouldia, Coprosma, Psychotria
Labiatae	100+	Phyllostegia, Stenogyne
Rutaceae	100±	Pelea, Zanthoxylum
Loganiaceae	75±	Labordia
Euphorbiaceae	75±	Euphorbia (subgen. Chamacsyce)
Gramineae	65+	Panicum, Eragrostis
Cyperaceae	50+	Cyperus
Pittosporaceae	50±	Pittosporum
Piperaceae	50±	Peperomia
Caryophyllaceae	45±	Schiedea

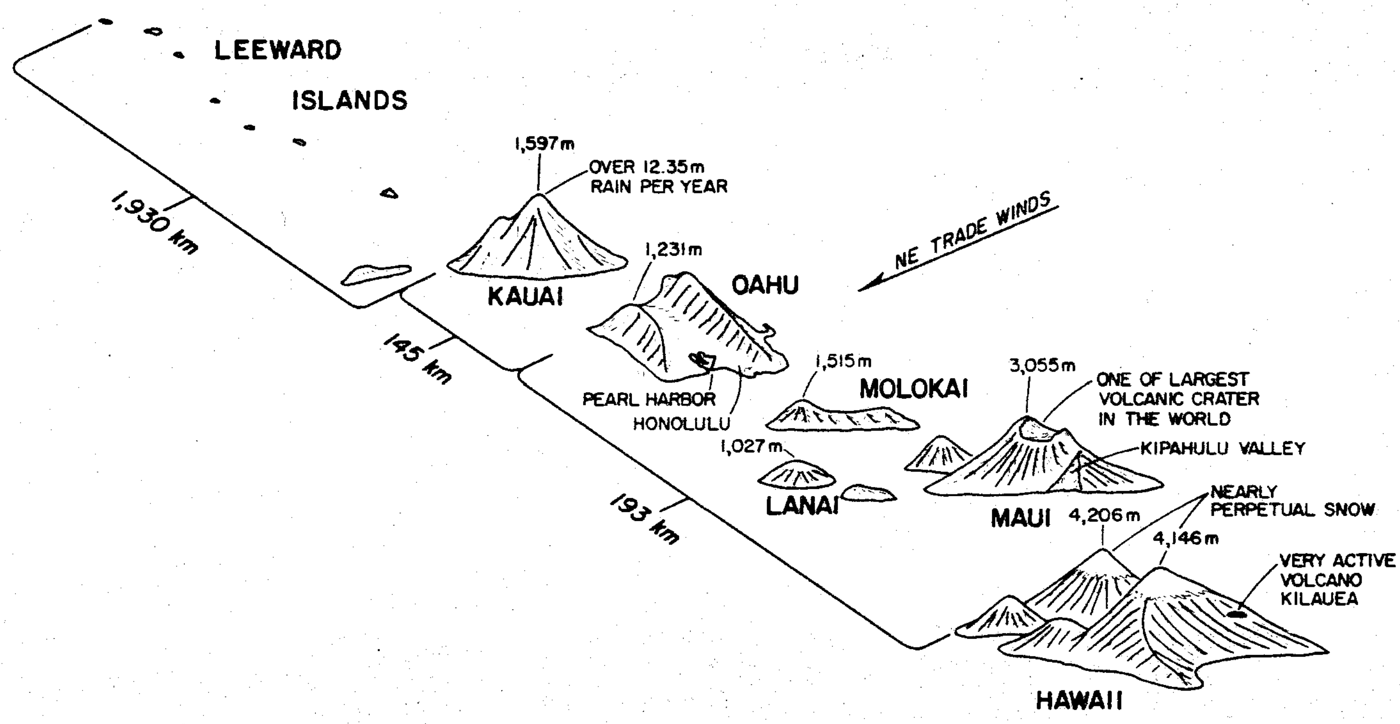


FIG. 3.3. Generalized topographic profile of the Hawaiian Islands.

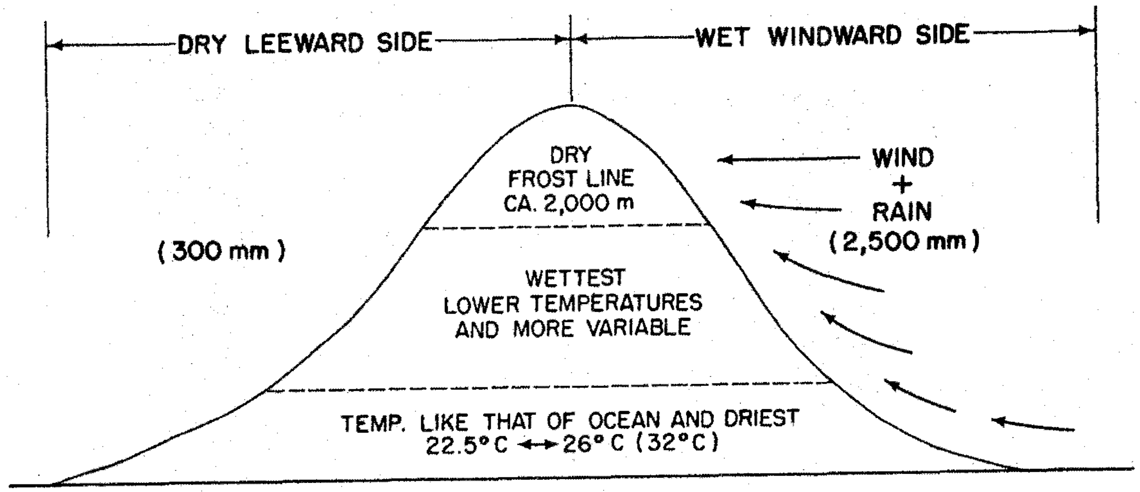


FIG. 3.4. Generalized climatic cross-section through the higher Hawaiian mountains.

3.4 Soils

The soils in the Hawaiian Islands have developed from volcanic ash and basaltic lava under the wide range of climatic conditions described in the previous section. Another soil area in some coastal sections and in the Leeward Islands has developed from marine deposits, such as coral limestone and sand. Cline et al. (1955) give an excellent description of the Hawaiian soils according to the earlier system of Great Soil Groups. This is now superseded by the 7th approximation to a new comprehensive system of soil classification (Soil Conservation Service 1960). However, certain general relationships are unaffected by the new system: the Hawaiian soils are at least as varied as the climatic zones in Hawaii, and they are not unique but can be related closely to similar soil types elsewhere in the tropics.

This means that soils developed in humid tropical lowlands to mid-altitudes on the windward sides are laterites. Laterites are characteristically reddish brown (because of *in situ* ferric iron precipitation) deeply weathered soils, low in silicates and cations, and of weakly acid to strongly acid reaction. Soils developed in dry climates (mostly on the leeward sides) are often lighter in color, less strongly leached of cations, even partly calcified, and of less acid to circumneutral reaction. Most of the soils in high altitudes are geomorphologically recent and poorly or incipiently developed from parent materials. On steep slopes, soils are also poorly developed because erosion keeps pace with weathering, constantly removing soil particles and layers developed from the parent materials.

The Hawaiian soils were remapped recently according to the new comprehensive system of soil classification (Sato et al. 1973 for Hawaii Island; Foote et al. 1972 for all other high islands). A general summary was provided by Uehara (1973). Ten soil orders are recognized for the Hawaiian Islands following the new system. These may be grouped into three broader environmental categories (A, B, C) as shown in Table 3.1.

3.5 Flora

The terrestrial native flora of the Hawaiian Islands is remarkable. It contains about 1440 species of angiosperms (St. John 1973), 170 species of pteridophytes (Fosberg 1948), 160 species of liverworts (Miller 1956), 240 species of mosses (Bartram 1933, 1939; Hoe 1974), 700 species of lichens (Magnusson 1954), and an unknown number of algae and fungi. Endemism is extremely high, especially in the vascular flora. Over 96 percent of the native species of angiosperms are endemic, as are about 65 percent of the pteridophytes, 75 percent of the liverworts, 65 percent of the mosses, and 38 percent of the lichens. Although the fungi and the terrestrial and freshwater algae have not been thoroughly studied, it appears that they exhibit little, if any, endemism. No endemism seems to be present in the blue-green algae recorded from any habitats in Hawaii.

The vascular flora has apparently been derived from a relatively small number of species which reached the Hawaiian Islands by long-distance dispersal. An estimated 272 original successful immigrants could have given rise to the native angiosperm flora, while 135 immigrants could account for the pteridophyte flora (Fosberg 1948). In Hawaii today one finds expressed in the flora all stages of evolutionary development: widespread genera with some species only slightly or not at all different from representatives elsewhere in the world, widespread genera with many distinct and well-defined endemic Hawaiian species, and genera which are endemic.

The affinities of Hawaii's flora seem to be primarily with areas west and south of the Hawaiian Islands with surprisingly little affinity with the nearest continental area, North America. Fosberg (1948) estimates that of the original immigrants of the angiosperms, 40.1 percent show affinities with the

Indo-Pacific region, 16.5 percent show affinities with the Austral region, 13.3 percent show affinities with the American region, and 12.5 percent show Pantropic and Cosmopolitan affinities. Among original pteridophyte immigrants, 48.1 percent show Indo-Pacific affinities, 20.8 percent show Pantropic and Cosmopolitan affinities, and 11.9 percent show American affinities. While additional studies will contribute information which may change the percentages expressed above, the overall pattern of affinities exhibited by the flora seems fairly clear, and is unlike that of any other area in the world.

In terms of largest numbers of well-recognized species and varieties, some of the best-represented families of angiosperms are tabulated in Table 3.2.

The native flora is a disharmonic one, and several plant groups which are widespread in the tropics and might be expected to be native in Hawaii are not. Fosberg (1948) considered the following groups to be "significantly absent" from the native flora: *Ficus*, *Piper*, Cunoniaceae, Bignoniaceae, Araceae, Gymnospermae, and mangroves. All of these groups except the Cunoniaceae have been introduced to Hawaii in some numbers in recent years. Mangroves have been successful, probably because there were no other plants occupying their particular ecological niche. In less than 50 years mangrove swamps have developed on Molokai, Oahu, and Lanai. A few species of *Ficus* (Moraceae) and *Spathodea campanulata* (Bignoniaceae) have become naturalized to some extent, but usually only in otherwise disturbed areas. They are not yet causing serious problems. *Piper methysticum* has persisted in the wild since its cultivation by the Polynesians. Other than these, the plants in the groups "significantly absent" from the native flora have not seemed to spread beyond cultivation.

The most successful species of the introduced flora are those which have become thoroughly naturalized, have extensive distribution ranges, and most often seem to be in competition with the native flora. They include: *Prosopis* pallida, Leucaena latisiliqua, Acacia farnesiana (Leguminosae); Lantana camara, Stachytarpheta spp. (Verbenaceae); Rubus rosaefolius, R. penetrans (Rosaceae); Psidium guajava, P. cattleianum, Rhodomyrtus tomentosa, Eugenia cumini (Myrtaceae); Myrica faya (Myricaceae); Melastoma malabathricum, Tibouchina semidecandra, Clidemia hirta (Melastomataceae); Opuntia megacantha (Cactaceae); Bidens pilosa, Pluchea spp., and many other genera (Compositae); Commelina diffusa (Commelinaceae); Andropogon glomeratus, A. virginicus, Panicum maximum, Paspalum conjugatum, Pennisetum clandestinum, P. setaceum, and many other genera (Gramineae).

Although many monographic treatments of genera and families of Hawaiian plants are available, the only comprehensive manual of the Hawaiian flora was published by Hillebrand in 1888 (the 1965 facsimile edition is widely available). This manual is badly out of date, and treats only about 1000 species. Rock's (1913) flora of the native trees is limited to selected species, but is still very useful. Neal's (1965) garden flora provides brief descriptions and some keys for many of the cultivated and introduced weed species. Degener's Flora Hawaiiensis (1932 - present) is not yet completed. It treats a little over half of the native species only. A comprehensive checklist of the flowering and seed plants in Hawaii has recently been produced by St. John (1973). According to his estimate the number of seed plants in the Hawaiian Islands is: 2,744 native species and varieties and 4,987 introduced species and varieties. Of the exotic taxa, 1 percent are now growing in wildland habitats.

3.6 Vegetation

The wild vegetation in the leeward lowlands consists mostly of introduced plants. Here, in this warm, tropical winter-rainfall and summer-drought climate one can distinguish several structural formations. Most typical is the perennial grass savanna. The more dominant grasses are Heteropogon contortus and Rhynchelytrum (Tricholaena) repens. The woody plants may be scattered trees or shrubs, or shrubs variously clumped, often forming thickets. Among trees, members of the Leguminosae are important, particularly Prosopis pallida and Leucaena latisiliqua.

Open seasonal evergreen scrub and forest occur above this lowland vegetation on the leeward side. Where well-preserved (a few places only), this is taxonomically quite a rich tree vegetation, with at least 20 native tree species. Among the more common ones are Sapindus oahuensis, Diospyros sandwicensis, Erythrina sandwicensis, and Canthium odoratum. However, most of this subhumid, summer-dry environment is converted to introduced vegetation showing variously open grass-shrub, shrub, and tree vegetations. Among the quantitatively more important exotic trees are Psidium guajava, Schinus terebinthifolius and Eugenia cumini.

In the montane environment, evergreen rain forest predominates with Myrtaceae (Metrosideros, also the introduced taxa Eugenia spp. and Psidium spp.) and native tree ferns (Cibotium spp.). The native legume tree Acacia koa prevails locally in patchy stands in the submontane part of the rain forest zone. The wettest parts of this zone contain bogs on gently sloping or level terrain. One example is the Alakai Bog on Kauai with dwarf forms of the Metrosideros tree and Cheirodendron spp.

The rain forest vegetation reaches to the highest elevations on Kauai (1590 m), Oahu (1230 m), and Molokai (1500 m). On the two higher-mountain islands, Maui (3055 m) and Hawaii (4206 m), the rain forest vegetation is replaced upwards (at about 1700 m) by mountain parkland or savanna. There, native legume trees are again important (Acacia koa, Sophora chrysophylla). Above this occurs subalpine open forest and scrub. The scrub shows "heath," that is, shrubby members of Ericaceae (Vaccinium spp.) and those of a closely related family, Epacridaceae (Styphelia). In the alpine scrub and near the tree line (on Mauna Kea near 2800 m) one may find individuals of the peculiar herbaceous phanerophytes, the silverswords (Argyroxiphium spp.). This genus is found only in Hawaii. Homologs in the tropical Andes are the giant espeletias, and on Kilimanjaro, the treelike senecios. These three taxa are all from the family Compositae. Above the alpine scrub is the alpine tundra or stone desert. On Mauna Loa the alpine tundra extends from 3000 m to the summit. On Mauna Kea it extends from 4000 m to the summit. The alpine tundra is characterized by a sparse moss (Rhacomitrium lanuginosum), by crustose lichens (e.g., Lecanora spp.), or by both.

This general sequence of altitudinal zonation is quite similar to that on several continental tropical mountains (Walter 1971). However, the floristic communities are very different. Hawaiian vegetation zones have been described by several authors including Hillebrand (1888), Rock (1913), Egler (1939), Ripperton and Hosaka (1942), Krajina (1963), and Knapp (1965). A summary comparison of three of these zonation schemes is shown in Table 3.3.

Floristic communities have been identified by Fosberg (1961, 1972) on a very general level. He recognizes about 30 major ecosystems for Hawaii. On a more detailed (i.e. larger scale) level, Hatheway (1952) and Wirawan (TR 34) described floristic communities for the native dry forest remnant on Oahu. Various other vegetation segments have been studied floristically for their community formation and ecology. These segments include the coastal communities on Oahu (Richmond and Mueller-Dombois 1972), the dry-grass communities on Oahu (Kartawinata and Mueller-Dombois 1972), the dry-zone vegetation on Oahu (Egler 1947; Mueller-Dombois and Spatz 1975), the east flank vegetations on Mauna Loa and Mauna Kea (Mueller-Dombois and Krajina 1968), the vegetation in Hawaii Volcanoes National Park (Mueller-Dombois 1966; Newell 1968; Mueller-Dombois and Fosberg 1974), and the vegetation on recent volcanic materials (Atkinson 1969, 1970; Eggler 1971; Smathers and Mueller-Dombois TR 10).

TABLE 3.3 Ecological zones in the Hawaiian Islands: a summary comparison of three zonation schemes

F. Egler (1939)	R. Knapp (1965)*	V.J. Krajina (1963)
Xero-tropical	I. Hot dry zone	Important key species
Makai zone (seaward)	4. Very dry	1. *Prosopis* (kiawe) zone
Middle zone	3. Moderately dry	2. *Leucaena* (koa haole)
		3. *Psidium* (guava) - *Lantana*
Mauka zone (inland towards the mountains)	5. Zones 3 and 4 mixed; Niihau and Kahoolawe	
Pluvio-tropical	II. Rain forest zone	
guava zone	1. Submontane	4. *Acacia koa* - *Psidium* - *Styphelia* (koa - guava - pukiawe)
koa zone		5. *Acacia koa* - *Nephrolepis* - *Paspalum* (koa - Boston fern - Basket grass)
ohia zone	2. Montane	6. *Metrosideros* - *Cibotium* (ohia - tree fern)
		7. *Cheirodendron trigynum* - *Cibotium* (olapa-tree fern)
cloud zone		8. *Cheirodendron dominii* - *Clermontia* - *Gunnera* (lapalapa-oha-wai-ape'ape)
		9. *Oerobulus* - bog zone (Alakai swamp and others)
Only on Maui & Hawaii	III. Cool dry-forest and heath zone	10. *Metrosideros* - *Sadleria* (ohia - amaumau fern)
	6. Upper montane or subalpine	11. Koa - Boston fern - *Dryopteris paleacea*
		12. Koa - *Sophora* (mamane) - *Styphelia* (pukiawe)
		13. *Sophora* - *Styphelia* - *Vaccinium* (ohelo)
	IV. Alpine	
	7. Cold desert, from about 3000 m up	14. Lichens, mosses, (*Argyroxiphium*)

* Number sequence relates to vegetation zone map in Knapp (1965: 320).

Note: In addition a strand zone is present on all islands. It covers most of the leeward islands in their entirety.

3.7 Land Arthropods

With the relative paucity of species and individuals of vertebrate animals in the native fauna of Hawaii, the arthropods assume great importance in the terrestrial biota from the standpoint of dominance in numbers of species, numbers of individuals, and ecosystem function. There are more than 5,000 endemic species of land arthropods already described or sorted for studies in progress. The total number will be considerably larger, although many species are facing extinction with the current rapid change in the environment.

The insect fauna of an area is closely associated with the native vegetation. This is more true for Hawaii than for continental areas for several reasons. Because the Hawaiian archipelago is extremely isolated, natural immigration to the islands has been highly selective. The subsequent naturalization probably results in an even greater selectivity. Primary colonizers must have been plants; but the pattern of later successful colonization by plants was influenced by the arrival of pollinators, including arthropods. These first plants were probably followed by insects of several types, largely feeders on living, freshly decaying, or dead plants. Because of the few vertebrate animals colonizing, those groups parasitic on vertebrates, and living in their nests, cadavers, and droppings, are few in number. Insects parasitic and predaceous on other insects must have come secondarily or evolved from already established species. Insects with narrow host-requirements were less likely to establish themselves. Such species are better known from intentional introductions for biological control of pests.

In the course of their evolution since reaching these islands, the native insects have to a great extent become fully dependent upon endemic plants, often in a very narrow host relationship. With the advent of more and more introduced plants, there has been rather little evidence for the attachment of endemic insects to introduced plants. Thus the native fauna becomes restricted in occurrence or extinct as its plant associates are affected by man and introduced biota.

Table 3.4 is a summary of the presently known endemic Hawaiian arthropods. Many of the endemic species belong to the principal phytophagous groups (Heteroptera, Homoptera, Lepidoptera, and Coleoptera). Many others belong to groups feeding in decomposing plants (especially Diptera; many Coleoptera). Hardy (personal communication 1974) estimates that when all species are known, the actual number of endemic insect species (except for the Diptera) will be much larger than the figures given in Table 3.4. Hardy estimates that there are 8,000 - 10,000 species of endemic insects.

The disharmonic nature of the endemic arthropod fauna left vacant ecological niches. These niches were often filled by adaptive shifts in the groups present (for example, a shift from phytophagous to predaceous forms). More recently, arthropods introduced by man have filled these niches. By adaptive shifts these exotic arthropods often displace endemic species. Ants, mosquitos, termites, and cockroaches are lacking in the endemic fauna; but several species of each are now well-established and have had great impact on both the human economy and the endemic biota.

Among the insects proper, 33 orders are recognized. Only 15 of these are included in the native fauna. Thirteen additional orders have been introduced by man. Man has introduced about 1500 species of insects as well as some 200 kinds of mites and other arthropods.

3.8 Land Snails

Since the first decade of this century the Hawaiian land snails, especially tree snails of the family Achatinellidae, have been cited as classic examples of the results of evolutionary phenomena.

Of the two best-known families, the Achatinellidae and Amastridae, the latter is the more primitive and probably the older of the two in the islands. The amastrids are predominantly ground snails, feeding on decaying vegetation and fungi. They are both oviparous and viviparous. Most are dull and inconspicuous in color, but in shell form they exhibit remarkable diversification. The largest members of the family Amastridae--*Carelia*--may reach 85 mm in length. *Carelia* are now confined to Kauai; but fossils have been found on Niihau. Smaller, more elaborately sculptured amastrids occur on Oahu, Maui, Molokai, Lanai, and Hawaii.

The nine families of native Hawaiian land snails are represented by 37 genera and some 1000 species and subspecies. Of these, four genera and 215 species and subspecies belong to the family Achatinellidae.

The Achatinellidae are, for the most part, highly colored and viviparous. They feed on fungi and on decaying vegetation on the leaves and trunks of trees. No achatinellids are known from Kauai. On Oahu, Maui, and Molokai they have differentiated into several genera and hundreds of specific entities, some apparently confined to particular ridges and valleys (Baldwin 1887, Hyatt 1912 - 1914).

Introduced land snails and slugs are primarily of concern as agricultural pests in most regions of the world. In Hawaii introduced snails are not only agricultural pests, but they also decimate the native land snail fauna and act as intermediate hosts for a number of parasites. Disruption of the native land snail fauna stems from the introduction of the giant African snail, *Achatina fulica*, on Maui and Oahu in 1936. Efforts to eradicate the snail failed, and in 1957 carnivorous snails from a variety of countries were introduced in an attempt at biological control. Of 23 species representing 14 genera introduced at that time, at least two have become widely established: *Gonaxis quadrilateralis* and *Euglandina rosea*. *Euglandina*, which in its native habitat in Florida preys on tree snails, has moved into Hawaii's native forests

TABLE 3.4 Tentative summary of endemic Hawaiian terrestrial arthropods*

Order	Families with Endemic spp.	Genera with Endemic spp.	Endemic Genera	Endemic Species
Pseudoscorpionida	?	?	?	?
Acarina	sev.	?	?	100+
Araneida	10	28	8	100+
Amphipoda	1	4+	2+	30+
Isopoda	1	1	-	1+
Symphyla	1	2	-	2
Diplopoda/Chilopoda	1	1	-	15
Palpigrada	1?	1?	?	?
Tardigrada	1?	1?	-	?
Collembola	1	1	-	1+
Thysanura	1	1	-	2
Orthoptera	2	7	6	50+
Dermaptera	1	?	?	2+
Psocoptera	3?	3	2	200
Mallophaga	2	3	-	5
Odonata	3	3	2	29
Thysanoptera	3	6	3	30
Heteroptera	11	37+	25+	650+
Homoptera	5	32	21	352+
Neuroptera	3	6	5	54
Lepidoptera	20	93	47	863+
Coleoptera	19	102	71	1500
Diptera	26	84	12	1500+
Hymenoptera	15	44	30	710+
Totals**	126	458	234	6196

* Based on published volumes of <u>Insects of Hawaii</u> by Zimmerman (1948a-e, 1957, 1958a-b) and Hardy (1960, 1964, 1965), with estimates of additions based on existing collections and on recent discoveries by the US/IBP Island Ecosystems Stability and Evolution subprogram.

** Totals do not include figures with question marks.

where it is a serious threat to the tree-dwelling Achatinellidae.

Other mollusks introduced either accidentally or on purpose are of less significance to the native biota: Bradybaena similaris and the slugs Dendroceras laeve and Veronicella alte are common garden pests, and Bradybaena, Opeas javanicum, Subulina octona, Dendroceras, and Veronicella are hosts for the rat lungworm.

3.9 Land Birds

Hawaii now has two groups of land birds: endemic and exotic. Seven families of world birds have endemic genera, species, or subspecies in Hawaii, and an eighth family (Drepanididae, Hawaiian honeycreepers) is endemic to the Hawaiian Islands.

The honeycreeper family is one of the most spectacular examples of adaptive radiation among animals. Plumage colors in the subfamily Psittirostrinae range from dull olive-drab to bright yellows and oranges. Bill shapes range from heavy parrotlike and finchlike to short, slender warblerlike to extremely long and decurved types. In the subfamily Drepanidinae plumages are pure or some combination of white, black, scarlet, and vermillion. Bill shapes vary in length, always decurved. Although definitive studies remain to be done, it is clear that niche differentiation, especially with respect to feeding, is equally as spectacular as morphology. In Hawaii the Drepanidids alone have filled ecological niches that, in continental ecosystems, are not filled within a span of several orders of birds. For example, there are Drepanidids with feeding strategies similar to those of parrots, finches, warblers, woodpeckers, nectar feeders, and creepers.

From a presumed single ancestral colonizing species 23 species and 24 subspecies of honeycreepers evolved. Of these, seven species and seven subspecies of honeycreepers are thought to be extinct. An additional 22 species or subspecies are now classified as rare and endangered.

The other endemic birds are listed in Table 3.5. Of these endemic birds, seven species or subspecies are presumed to be extinct and six others are listed as rare and endangered.

Very little is known of the life history and ecology of any of the extinct birds. In recent years the nest and eggs of several endemic species have been described (Berger et al. 1969; Berger 1969a, 1969b, 1970), and studies of the breeding biologies of the Oahu Elepaio (Chasiempis sandwichensis gayi; Frings 1968), the Hawaii Amakihi (Loxops virens virens; Berger 1969a), and four honeycreepers on Kauai (Eddinger 1970) have been completed. An intensive study of the Palila (Psittirostra bailleui; van Riper TR) is now in progress. However, most of the endemic birds have not been thoroughly studied, and their habitats and populations continue to decline. Conant (TR) has begun a study of population dynamics in an attempt to define critical habitat on the basis of maximum density, frequency, and diversity of native bird species.

The introduction of parasites and diseases new to the Hawaiian avifauna is one of the most serious consequences of exotic bird introductions. The role of bird malaria, as well as avian pox and other parasitic infections, in the decline of the Hawaiian avifauna is unknown; but available evidence suggests that it is serious (Warner 1968).

The exotic Linnet (Carpodacus mexicanus) and Ricebird (Lonchura punctulata) are known to be important agricultural pests; yet new potential pests, such as the recently established Warbling Silverbill (Lonchura cantans) on Hawaii (Berger 1975), continue to be intentionally or accidentally introduced.

At present there is little evidence to demonstrate that exotic bird species compete seriously with native birds for ecological resources. However, the Japanese White-eye (Zosterops japonica) coexists with native birds where they are found, and it exploits many of the same food resources (Guest TR 29).

TABLE 3.5 Endemic Hawaiian birds other than honeycreepers

Family	Genus, species	Common Name
Accipitridae	Buteo solitarius	Hawaiian Hawk or Io
Strigidae	Asio flammeus sandwichensis	Hawaiian Owl or Pueo
Corvidae	Corvus tropicus	Hawaiian Crow or Alala
Turdidae	Phaeornis palmeri	Small Kauai Thrush
	Phaeornis obscurus	Hawaiian Thrush
Sylviidae	Acrocephalus f. familiaris	Laysan Millerbird
	Acrocephalus familiaris kingi	Nihoa Millerbird
Muscicapidae	Chasiempis sandwichensis	Elepaio
Meliphagidae	Moho braccatus	Kauai Oo
	Moho apicalis	Oahu Oo
	Moho bishopi	Molokai Oo
	Moho nobilis	Hawaii Oo
	Chaetoptila angustipluma	Kioea

The Japanese White-eye is probably the most abundant and widespread land bird in Hawaii. Studies of this species and other potentially competitive species are being conducted in habitats where they coexist with native birds. The aim is to determine whether or not they compete successfully with native birds and what the consequences of such competition are for the native avifauna.

3.10 Effects of Man on the Biota

The native Hawaiian biota, which had evolved in the absence of man and of large grazing or carnivorous mammals, seems to have been in a delicate balance within the island ecosystems before the arrival of man. About 1300 years ago, when the Polynesians first arrived, they brought with them some 25 species of plants for food, medicine, fiber, and other purposes. These included coconut, taro, banana, breadfruit, candlenut, paper mulberry, ti, sweet potato, and various yams. They also brought rats, dogs, pigs, and jungle fowl. The Polynesians, and the organisms which they brought with them, certainly influenced the native biota; but one can only speculate on the magnitude of their effects. Undoubtedly the impact of the Polynesians was greatest in areas where the Hawaiians lived and grew their crops. On the other hand, Hawaiians considered land, plants, and animals as the property of, and to be held in trust for, the gods. This outlook resulted in a form of practical conservation. When birds were trapped to obtain brightly colored feathers, this was said to be done without harming them, and they were later released to grow new feathers. Fish and shellfish were collected only in season. Thus, although the initial effects of Polynesian colonization on the native Hawaiian biota may have been great, they were certainly less drastic than the effects brought about by sustained contact with European cultures.

It is likely that new ecological equilibria were established at some time after the extensive colonization of the islands by the Polynesians, and that these equilibria were operative in 1778 when Captain Cook arrived.

Cook released the goat and a second breed of pig in 1778. In 1793 Captain Vancouver released cattle and sheep. Horses were introduced in 1803. Cats and commensal rats and mice probably arrived on some of the earliest ships. The last feral horses and cattle are still to be found in some areas of the Kona coast of Hawaii today. Sheep, goats, and pigs today endanger the native forests and other ecosystems on most of the main islands.

While the large hoofed animals were rapidly increasing in numbers, they degraded the vegetation over wide areas by feeding on the seedlings of native woody plants, by local overgrazing, and by trampling. Many plants were introduced intentionally and otherwise; and these occupied the areas newly opened up by animals. Since early records are so incomplete we cannot estimate the number of species of the native biota which became extinct in the century following Cook's visit. For the last hundred years better records are available. As extensive areas of land were cleared for agricultural purposes the native biota disappeared almost completely from these areas.

The delicate balances existing in the native biota were easily upset. As the plants disappeared the birds, insects, and terrestrial mollusks which were associated with them also disappeared.

Man has intentionally and unwittingly introduced to the islands fauna that have adversely affected the native biota. Introduced species of land snails and slugs continue to threaten endemic land mollusks. Introduced birds, and the parasites and diseases carried by them, have seriously affected the native birds (Warner 1968). Certain introduced insects are important in the spread of these bird diseases and parasites. Additional species of insects and other arthropods are accidentally introduced each year (Beardsley 1962). Exotic arthropods affect not only the endemic biota, but also the human economy. These man-caused biological perturbations present a constantly growing and changing problem.

Even after the exceptional biotic resources of Hawaii came to be appreciated by the scientific community, the desire for "progress" and economic development on the part of the general public was, and still is, so great that policies to protect and manage Hawaii's unique and most precious resource--its native biota--are only slowly being put into effect.

CHAPTER 4

ORGANIZATION OF INTEGRATED RESEARCH

4.1 Organism Groups Studied in the Program

A major interest of the project participants was the study of well-preserved Hawaiian ecosystems with a dominance of native species. We felt that the opportunity to study these species was decreasing. Moreover, we thought that studies of well-preserved ecosystems would provide basic information against which we could compare ecosystems variously disturbed by the invasion of exotic species.

Plants, arthropods, and birds received the greater emphasis, because most of the native species are found in these categories. A few species from each category were selected for studies in microevolution and genecology. The more cosmopolitan groups, the fungi and terrestrial algae, were also studied. Among insects and other arthropods the groups emphasized were Diptera (particularly Drosophilidae and Sciaridae), Coleoptera, Heteroptera, Homoptera, Lepidoptera, and Acarina. Other arthropods were included according to their ecological role, such as pollinators, seed feeders, and ectoparasites. Notable gaps that could not be filled because of limited funds were, among botanical organisms, the bryophytes and lichens and, among animals, the snails.

A general aim was to study the ecological roles of these organism groups in selected ecosystems. This included a consideration of interactions between native and man-introduced species. Therefore, exotic species were also studied in each category and special emphasis was given to introduced mammals, particularly to the impact of rodents (rats, mice, mongooses) and feral ungulates (goats, pigs) on the vegetation.

The time constraints of the project precluded a uniform advance of knowledge on the functional role of each organism group. Some of the groups required a considerable amount of taxonomic background work. However, our synthesis aim was to develop a unified basis. We accomplished this by concentrating our efforts for this project primarily on the structural (rather than the functional) aspects of ecosystem analysis. The main synthesis areas covered by this approach relate to (a) distribution and quantitative composition of species along spatial gradients, (b) population fluctuations in relation to phenological events and annual variations in climate, (c) community structure and niche differentiation in selected ecosystems, and (d) genetic structure and variation of selected populations.

The full elucidation of the ecological role of each species and species group can be considered a further step for which the groundwork has been laid.

4.2 Conceptual Modelling

The problem of bringing studies on organism groups together into an integrated approach is not as easy to solve as one may expect. The US/IBP Biome studies on the American continent had focused their research on ecosystem metabolism. For such functional studies there was a relatively simple model: the primary production - consumer - decomposer - mineral cycling processes of an ecosystem. These component processes provided a reasonable conceptual vehicle for organizing ecosystem research in most IBP teams.

In contrast, the focus of our program was on studies of species interactions in an evolutionary and ecosystem context. We set for ourselves the particular goal of finding out what there is, if anything, that makes island ecosystems different from continental ecosystems. We expected few differences in the gross functions of primary production, decomposition, and mineral cycling. The measurement of rates of photosynthesis and respiration, for example, of an island evergreen tropical montane rain forest was not expected to be greatly different from a continental evergreen temperate montane rain forest, except for the climatic variables involved. Of course, a major difference was to be expected in the consumer component of the island forest, largely because this ecosystem component evolved without the mammalian herbivores.

The study focus on species interactions had to be brought first into a framework of ecosystem structure that was useful to everyone on the program. We selected two ecological models for this purpose. These were (1) environmental gradient analysis and (2) structural community analysis.

Environmental gradient analysis along a major mountain slope provided us with a model to study the spatial variation of species and species groups in relation to one another and to known variations in habitat factors. The model was useful for investigating the quantitative relationships and spatial positions of native and introduced biota, for contrasting wide- and narrow-ranging species, and for defining degrees of adaptation to specific segments along the gradient. Time variations include such phenomena as phenological events and cyclic variations in soil fungi and algae populations.

Structural community analysis in a large, homogenous, relatively undisturbed montane rain forest provided us with a model to study the population structure of important organism groups and, in part, their niche differentiation in the forest. This gave us indices for predicting the dynamics of this important native island ecosystem.

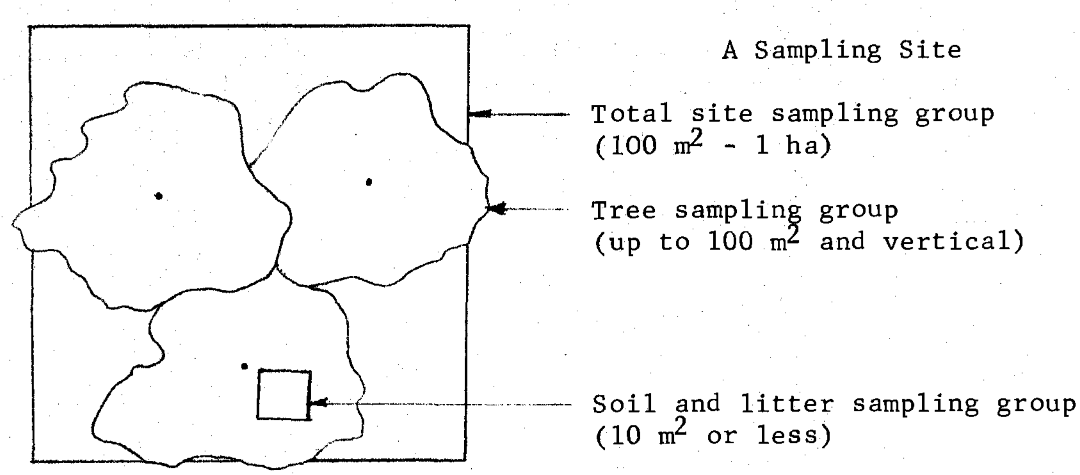
4.3 Site Coordination

We achieved integration by coordinating our research in two sites: the mountain slope and the rain forest. Each participant was required to sample according to a specified layout in these sites. The layout involved 14 focal sites along the mountain slope and four specified transects in the rain forest. Once he had contributed to the IBP site studies, each participant was free to investigate other sites deemed important for the study of his particular organism group. But the requirement for participation in our team research was to contribute to the two primary IBP sites.

We developed a hierarchical sampling scheme that was related to the size and general environmental sensitivity or behavior of our respective organism groups. On this basis, we recognized three sampling groups:

1. The soil and litter sampling group. This included the participants concerned with the soil and litter fungi, the soil algae, the soil arthropods, and the litter-inhabiting Diptera.
2. The tree sampling group. This included the participants concerned with phytophagous insects in general, with *Metrosideros* psyllids, *Acacia koa* psyllids, and the cerambycid bark and stem beetles.
3. The total site sampling group. This included the participants concerned with vascular plants, rodents, birds, and general habitat insects.

Because our sampling levels were hierarchical in size, sampling group 1 was to be included within sampling group 2, and group 2 within group 3. The basis for this was to attain a reasonable homogeneity across the three sampling levels so that group 1 sampling was meaningful in the framework of group 2 sampling, and group 2 sampling was meaningful in the framework of group 3 sampling. The following sketch illustrates what is meant by hierarchical integrated sampling.



4.4 Sampling and Data Processing

Data analysis and processing was built into the sampling scheme. For example, the mountain slope sampling data always involved the collection of three parameters: (1) the sampling location and date, (2) the species recorded, and (3) the quantity of each species recorded. These three parameters lent themselves to computer processing by the two-way table technique and dendrograph methods. Similarly, time phase data were adapted to processing by the two-way table technique and for display in three-dimensional computer diagrams.

Four strategically placed climatic stations were operated throughout the duration of the research. The climatic data on rainfall, throughfall, temperature, and relative humidity (from hygrothermographs)were processed weekly and transferred to the computer. Various tabulations, useful for interpreting behavior of all organism groups studied, were printed periodically as individual sheets and technical reports. These were distributed to all participants.

4.5 Communication and Administration

During the first two years we held quarterly workshops involving all program participants. These workshops were filled out primarily with conceptual modelling. In the latter two years, we held workshops twice a year and an annual review symposium once a year (in November). In addition to presentations and discussions of methods and results, this meeting served to clarify the content for the annual progress report and budget renewal proposal. Between meetings we communicated by telephone and memoranda. There was no need to establish a newsletter, since nearly all program participants were from one of two institutions in Honolulu--the University of Hawaii and the Bernice Pauahi Bishop Museum.

A major communication item was our Technical Report series, which was established in December 1970. The first results appeared in February 1972--one and one-half years after we launched the program. After that, Technical Reports were produced more or less continuously, one or two every month. We continued the series during the synthesis phase until the end of the final funding year, August 31, 1975.

The Technical Report series served to communicate preprints or manuscripts, individual progress, and data sets important to members of our team. The inside cover of each report contains a notice stating that the information is of a preliminary nature and was prepared primarily for internal use in the US/IBP Island Ecosystems Program. Thus, a Technical Report was purposely not considered a publication. This was important because it allowed an author to submit his manuscript to a journal of his choice at his convenience. The customary time lag of one to two years from the time a manuscript is submitted to a journal to the time it is published would have defeated our efforts to rapidly communicate our results within the group. Moreover, production of a Technical Report guaranteed the author's title to a particular piece of research, an important consideration in a program of interfacing research segments involving a number of investigators.

We produced 250 copies of each report--an operation that involved one typist full time. Yet, the operation was small enough to be flexible; and it did not require a major expense. This number of reports, moreover, allowed for distribution to interested individuals and institutions (such as the Institute of Pacific Islands Forestry, the Hawaii State Department of Land and Natural Resources, the National Park Service, all other US/IBP programs, and a few international programs). All Technical Reports are now on microfiche and are available from the University of Hawaii Library. A list of titles of all Technical Reports is appended to this volume.

The program was administered by a scientific director, an assistant director, and an administrative assistant, all working out of the same office.

Two co-directors served as advisors. Additional office staff included a typist, a computer programmer, and, in the final year, a technical editor. At the research site, a site manager cared for the four vehicles (two with 4-wheel drive) and for the maintenance of the two small houses rented from the Park Service. He also serviced the four climatic stations, maintained the day-to-day liaison with the National Park Service, and gave general assistance to program participants. Communication to the research site was by telephone.

CHAPTER 5

THE RESEARCH AREA

5.1 Geographic Location

The IBP study sites are located on the Island of Hawaii in and near Hawaii Volcanoes National Park (Fig. 5.1). The Island of Hawaii, locally called the "Big Island," is approximately 100 km by 100 km in size (exactly 10,480 km^2). The IBP field quarters consisted of two small houses located in the service quarters area of the National Park Service, near the east end of transect 1 on Figure 5.1, at 1200 m (3950 feet) altitude. The field quarters could be reached by car from Hilo Airport within 40 minutes.

Among the six transects shown on Figure 5.1, transect 1 (on the east flank of Mauna Loa) was chosen as the test site for the integrated environmental gradient analysis. Fourteen focal sites were established along the Mauna Loa Transect. These sites range from 3050 m (10,000 feet) in very sparse alpine scrub down to 1190 m (3900 feet) in the montane rain forest. The other five transects served as validation sites or for extension of individual studies. A second site for integrated sampling was established as an 80 ha (200 acre) plot at the north end of transect 2 (Fig. 5.1), near 1520 m (5000 feet) altitude. This site is outside the Park, in a well-preserved native rain forest in the Kilauea Forest Reserve. The site was reached by a 10-mile (16 km) long jeep trail leading through a cattle ranch.

5.2 Reasons for Choice of Area

A major reason for choosing this area was the availability of a site-preparation study entitled "Atlas for Bioecology Studies in Hawaii Volcanoes National Park" (Doty and Mueller-Dombois 1966). This 507 page document includes a checklist of vascular plants, a vegetation map with vegetation profiles, a description of the air-photographic coverage, the geology and volcanic events,

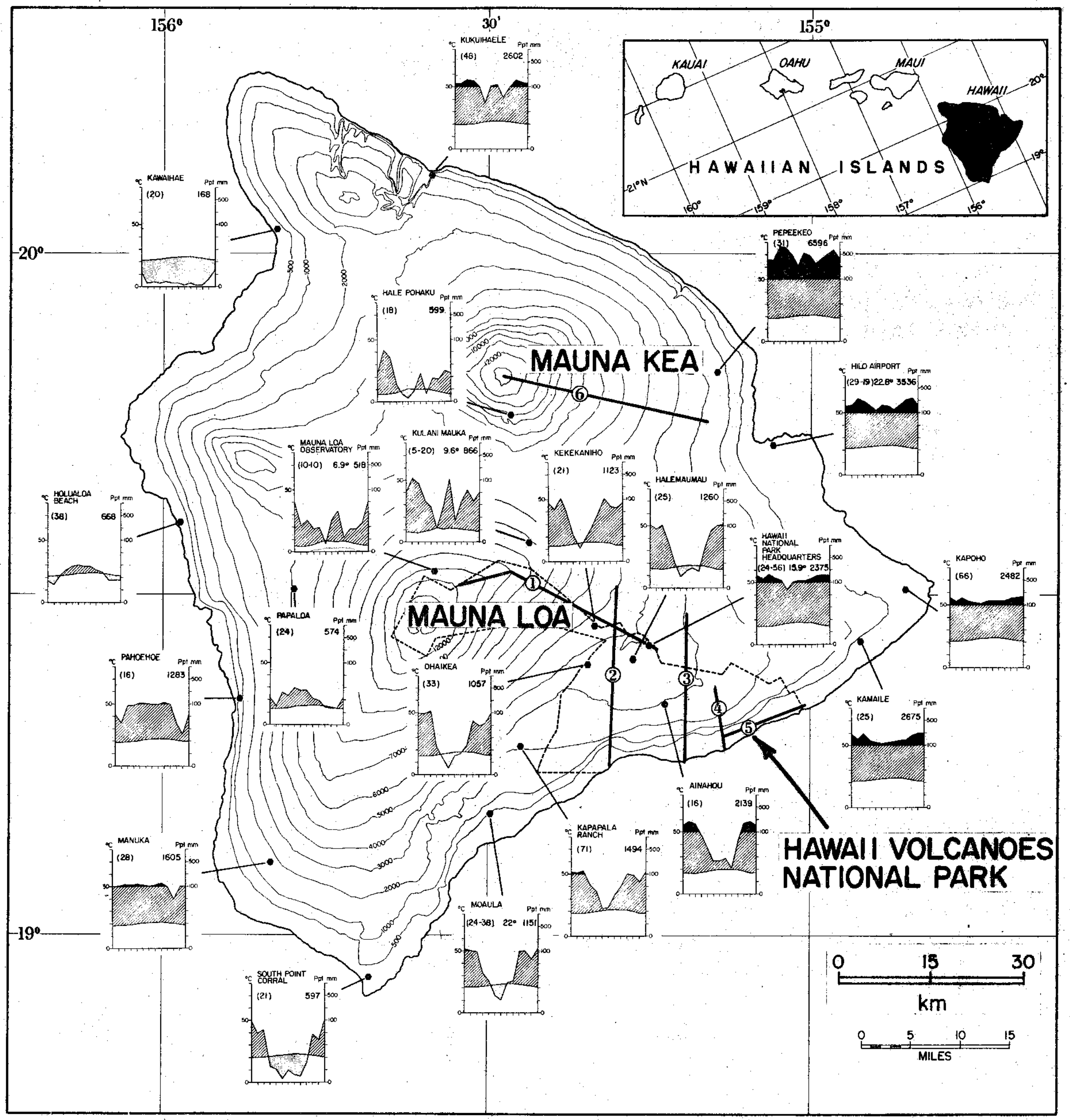


FIG. 5.1. Orientation map of Hawaii showing location of IBP transects 1-6. Transect 1 on the east flank of Mauna Loa was chosen as the test site for the integrated environmental gradient analysis. The 80 ha Kilauea rain forest study site is at the north end of transect 2. Dashed lines show outline of Hawaii Volcanoes National Park. Contour lines are given in feet. IBP field quarters were near the east end of transect 1. The diagrams show mean monthly rainfall (mm) and temperature (°C) curves plus mean annual rainfall of 21 weather stations.

the soils, the weather and climate, and a summary review of the biological studies done so far in the area, together with a bibliography.

Other reasons included the availability of relatively undisturbed sites still in original vegetation, the improved protection from vandalism of field instrumentation inside the Park, and the expressed interest of the National Park Service in having the IBP study done within its territory and of the private land-holding Bishop Estate Corporation in having a study done in the Kilauea Forest Reserve. Finally, there were important logistics advantages to choosing Hawaii Volcanoes National Park. We were offered field living quarters, laboratory, library, and herbarium facilities.

5.3 Characteristics of the Area

The area is geologically special in that it is within the range of active volcanism. The soil substrates are all still relatively recent volcanic surfaces. The last lava flow from Mauna Loa occurred in 1950. The Kilauea Volcano (at 1200 m) in the center of Hawaii Volcanoes National Park is almost continuously active. Thus, all results from our studies have to be interpreted with respect to a geologically very young mountain system. This, however, lends itself to interesting comparisons to older volcanic mountainous islands occurring in similar climates. In Figure 5.1 the climate of the study area is shown in relation to the rest of the island by 21 climate diagrams prepared according to the method of Walter (1971).

On the diagrams, the mean monthly air temperature is plotted with reference to the left-hand ordinate, resulting in the nearly horizontal curve on each diagram. The temperature intervals on the left ordinate are 10°C, starting with 0°C at the abscissa. The abscissa indicates the months of the year, with January at both ends and July in the center. Mean monthly rainfall is plotted with reference to the right-hand ordinate. The intervals are 20 mm from 0 mm at the abscissa upwards to 100 mm. From 100 mm on upwards, each interval represents 200 mm. The amount of rain in excess of 100 mm is indicated by a black field (see eastern part of the island, Fig. 5.1). Wherever the rainfall curve (which is the more irregular curve on each diagram) undercuts the temperature curve at the selected scale (of rainfall/temperature = 2/1), a drought period is indicated (see diagrams on south and northwest sides of island). The mean annual rainfall in millimeters is written at the right-hand top of each diagram. The mean annual temperature appears as a figure to the left only for stations with temperature records.

The mean annual temperature near the top of transect 1 is 6.9°C. At this elevation (near 3350 m or 11,000 feet), groundfrost occurs each night throughout the year. At the east end of transect 1 (at 1200 m or 3950 feet) the mean annual temperature is 15.9°C. At sea level (Hilo Airport) the temperature is 22.8°C.

The month-to-month temperature curve indicates typical insular tropical climates at all elevations because of the small difference (4° - 6°C) between summer and winter temperatures. The mean annual temperature at the north end of transect 2 in the Kilauea Forest study site can be extrapolated as approximately 14°C. Rainfall in the Kilauea Forest site is similar to, though somewhat less than, rainfall at the Park Headquarters on transect 1. In the Kilauea Forest site rainfall is between 1800 and 2000 mm per year; and there is usually a short dry season in June, when the monthly rainfall can be less than 100 mm. Along the Mauna Loa Transect (transect 1), the rainfall decreases from about 2400 mm at its east end in the rain forest to about 500 mm at its upper end (near 3660 m or 12,000 feet) in the alpine moss (Rhacomitrium) desert. In addition to the overall decrease upslope, rainfall is particularly low during June. At the tree line (near 2440 m or 800 feet) rainfall is also markedly low in September.

The climate along the Mauna Loa Transect compares well with that along the Mauna Kea Transect (Mueller-Dombois and Krajina 1968). The climate diagrams show wet conditions on the east side of the island. Summer-drought climates occur in the south. The reverse of this--winter-drought climate--occurs on the west side at Holualoa Beach. A true desert climate occurs on the northwest side of the Big Island at Kawaihae (168 mm).

The vegetation of the study area has been described in the "Atlas for Bioecology Studies..." (Doty and Mueller-Dombois 1966). Further details will be presented in the other parts of this volume.

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